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Nutrient Storage, Retranslocation and Relationship of Stress to Nutrition

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I. INTRODUCTION

Trees accumulate nutrients as their biomass increases and this chapter describes distribution of nutrients in the tree and discusses the form in which

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they occur. Accumulation of relatively large quantities of nutrients provides trees with an opportunity for some independence of external nutrient supply, and the nutrients in various parts of the tree may be regarded as reserves. Retranslocation may satisfy an important proportion of a trees requirements for certain nutrients (see Chapter 3). The main paths of translocation in xylem and phloem are described, and the probable extent of retranslocation is examined. At present most of the evidence for retranslocation comes from difference in nutrient concentrations, or preferably contents, with time, in various organs and tissues, particularly leaves. Nitrogen has a major effect on productivity of forest trees, and so its metabolism and storage are described in more detail.

Plantation trees frequently show evidence of stress and often succumb to drought, cold or disease, and here the effects mineral nutrients have in increasing the tree's tolerance to these stresses is also examined. Effects of nutrient status on resistance to moisture stress is limited to work with seedlings, but some data exist for effects of nutrients on resistance of plantation trees to cold stress. There are many publications relating many effects of mineral nutrition to disease resistance in trees, but this complex field is only touched on here.

II. NUTRIENT DISTRIBUTION WITHIN THE TREE

Nutrient distribution within the tree is a function of biomass distribution and nutrient concentration within the various tissues and organs. As might be expected, individual nutrients have different distributions within the same tree (Table I).

A. Age

As trees age, there are changes in the way their total nutrient content is distributed. This is primarily related to changes in biomass distribution that occur with age and differences in concentration of nutrients in each component with age. Young trees have a high proportion of their biomass in foliage and this becomes progressively less as the proportions of bole and bark increase (Rodin and Bazilevich, 1967). Consequently the proportion of nutrient contained by the foliage tends to become less and the proportion contained in bole and bark becomes more with age (Wright and Will, 1958).

Age of foliage affects the distribution of mineral nutrients. In deciduous

Table I. Nutrient distribution within major parts of the tree as a percent of total content, total nutrient content and biomass of five species.

Species	Age (yr)	Foliage (%)	Branches (%)	Bole bark (%)	Bole wood (%)	Roots (%)	Total (kg ha^{-1})
				N			
Pinus sylvestris[a]	45	30	20	11	20	19	186
Picea glauca[b]	40	34	28	10	13	15	449
Pseudotsuga menziesii[c]	36	32	19	15	24	10	320
Betula verrucosa[d]	55	14	31	—	27	28	543
Quercus alba[e]	150	9	23	—	36	22	631
				P			
Pinus sylvestris	45	27	19	14	11	29	21
Picea glauca	40	42	27	13	8	10	64
Pseudotsuga menziesii	36	44	19	14	14	9	66
Betula verrucosa	55	12	35	—	32	21	34
Quercus alba	150	10	19	—	30	35	41
				K			
Pinus sylvestris	45	27	17	13	19	24	96
Picea glauca	40	34	31	12	13	10	254
Pseudotsuga menziesii	36	28	17	20	24	11	220
Betula verrucosa	55	22	23	—	32	23	200
Quercus alba	150	14	31	—	27	26	419
				Ca			
Pinus sylvestris	45	13	19	21	28	19	123
Picea glauca	40	32	27	20	10	11	809
Pseudotsuga menziesii	36	22	32	21	14	11	333
Betula verrucosa	55	6	28	—	42	24	651
Quercus alba	150	3	33	—	39	20	2,029
				Biomass (t ha^{-1})			
Pinus sylvestris	45	4.4	10.6	5.3	55.6	19.3	95.2
Picea glauca	40	17.4	34.6	10.8	88.0	34.0	184.8
Pseudotsuga menziesii	36	9.1	22.0	18.7	121.7	33.0	204.5
Betula verrucosa	55	2.5	28.7	—	134.5	49.8	215.5
Quercus alba	150	5.4	52.8	—	129.0	95.6	282.8

[a]Mälkönen, 1974, [b]Alban *et al.*, 1978; [c]Cole *et al.*, 1967; [d]Ovington and Madgwick, 1959b; [e]Rolfe *et al.*, 1978.

species, of course, there is an annual cycle with rapid accumulation of nutrients in foliage as the leaves flush and expand, followed later in the year with redistribution of some nutrients (section V, B) and finally, abscission with the loss of remaining nutrients. Conifers generally carry needles produced in several different years so that 4–13 annual age classes may be present (Turner and Singer, 1976). Consequently current needles of *Pseudotsuga menziesii* (Douglas fir) may only contain 25% N, 23% P, 33% K, 11% Ca and 22% Mg of the total in the foliage (Webber, 1977); although dry matter and N content of 1-year-old needles may sometimes be greater than that of current needles (Mälkönen, 1974) dry matter and content of nutrients generally declines in conifers, by as much as half, for each older class of needle.

Although less is known about distribution of nutrients in roots than in aerial parts of trees it appears that a large proportion of root system nutrients are found in the smaller, and presumably younger, roots (see Chapter 6). Root biomass varies from perhaps 10 to 40% of the total biomass, but values between 15–20% seem common (Santantonio *et al.*, 1977). The root system tends to contain nutrients in proportion to its biomass (Rodin and Bazilevich, 1967), and, in 33 year *Pinus sylvestris* (Scots pine), roots less than 0.5 cm in diameter amounted to 10% of the root biomass, but contained 41% of the root N and between 15 and 36% of the other macronutrients (Ovington and Madgwick, 1959a).

B. Species

The distribution of nutrients within the tree may vary according to species. Conifers tend to have a higher proportion of biomass in foliage than deciduous broadleaved trees and among conifers, spruces have proportionately more foliage than pines. Consequently a greater proportion of total tree nutrient content is found in foliage in conifers (20–25%) than in deciduous broad-leaved trees (8–10%) even though the nutrient concentration in conifer foliage is lower than in broad-leaved species (Rodin and Bazilevich, 1967). Comparison of 40-year-old trees growing on the same site showed that three conifer species contained a higher proportion of their total nutrients in foliage than did *Populus tremuloides* (trembling aspen) (Alban *et al.*, 1978). The foliar biomass of the conifers was 1.5 (*Pinus banksiana*; jack pine) to 4.8 (*Picea glauca*; white spruce) times greater than that of *populus tremuloides*, and the quantities of nutrients were greater in *Picea abies* (Norway spruce) (N 153, P 27, K 86 kg ha^{-1}) and *Pinus resinosa* (red pine) (N 131, P 19, K 59 kg ha^{-1}) foliage than in *Populus tremuloides* (N 87, P 9, K 47 kg ha^{-1}) foliage.

III. NUTRIENT STORAGE

Many organs and tissues within the tree contain reserves of nutrients which may be released, as the tissues mature or senesce, for reutilization in more actively growing regions. This may occur from foliage, bark and wood (e.g. Will, 1968). A proportion of the nutrients in old foliage or old sap wood may be regarded as a store which is reutilized elsewhere in the tree. Nutrients may also be stored as a result of an abundant external supply, as when fertilizer is applied. Current foliage readily reflects changes in nutrient supply and so, to a lesser extent, do inner bark and roots (e.g. van den Driessche and Webber, 1977b), and these presumably are the sites where surplus nutrients are stored, at least initially.

Miller *et al.*, (1979) have suggested nutrients are stored at two levels, the first being represented by recent uptake and including temporary seasonal storage. The second level consists of potentially mobile nutrients that can be used to make up for shortages of first level sources. According to this idea consumption of second level sources usually occurs at the expense of proper functioning of older tissues, and may result in growth reduction depending on the contribution of such tissue to growth. Since growth decline tends to be progressive with reduction in internal nutrient status the two levels of storage are probably not discrete.

Mobilization and use of stored nutrients can make the tree partially independent of uptake from external nutrient sources (see Chapter 3). In northern temperate regions deciduous trees develop leaves, often with maximum seasonal N and P content, in three or four weeks (e.g. Olsen, 1948). The large uptake demand which spring growth could impose for nutrients from the soil is avoided because trees mainly use stored reserves for spring growth, absorbing nutrients when conditions are suitable throughout the year. Hardwoods growing in Tennessee translocate nearly all the N, P and K into the foliage before the end of May, yet N uptake rate from soil only reaches its peak in June (Luxmore *et al.*, 1981).

A. Storage Sites

(1) Roots

It is well established that N is stored in roots of fruit trees, e.g. root tissue of dormant two-year-old peach trees may contain 60–80% of the N stored during winter (Taylor and May, 1967). There is some evidence that storage

of N also takes place in roots of other trees. For example, in *Pseudotsuga menziesii* roots, arginine level can become high in late winter, especially in trees well supplied with N, and fall rapidly at bud burst (van den Driessche and Webber, 1977a).

The proportion of nutrients in root systems of north temperate zone forest trees is not particularly large (Table I), but below-ground parts of *Eucalyptus* trees, to which the roots contribute substantially, contain 37–63% of the N and 19–39% of the P in the tree (Bowen, 1980). They also contain a large proportion of the elements K, S, Zn and Cu. To what extent these accumulated nutrients are utilized, either in above ground parts of the tree or to sustain the periodic flushes of fine root growth which tree root systems produce (Santantonia *et al.*, 1977) is unknown. A ^{15}N study of prairie grass suggested that one-third to one-half of the N in above ground foliage may be translocated to the root system during fall and reutilized in new shoot growth the following year (Clark, 1977). However evidence for this type of storage function for tree roots is generally lacking.

The trace elements Cu, Zn and Fe may accumulate in the roots of seedlings. For example, Cu may accumulate in *Pinus radiata* (radiata pine) roots, and, under conditions of shortage the Cu stored in the roots is released to shoots (West, 1979). However, accumulation of Fe in roots of *Pinus sylvestris*, *Picea sitchensis* (Sitka spruce) (Nelson and Selby, 1974) and *Pseudotsuga menziesii* (van den Driessche, 1978) seemed due to internal chelation or precipitation rendering the element largely unavailable for shoot growth. It has been noted that Cu and Zn can accumulate in sweet orange seedling roots, primarily in the endodermis (Smith, 1953).

Roots must be important nutrient storage sites when coppicing is practiced, and in *Pinus elliottii* var. *densa* during its "grass stage". The possibility that *Eucalyptus* lignotubers function as nutrient storage sites, as well as storing carbohydrate, has long been recognized (Beadle, 1968).

Nutrients may accumulate in root systems as a result of absorption during a period when the shoot is dormant or inactive. Fruit trees generally absorb N during autumn and winter, provided soil temperature is above freezing, but this N is not translocated to the shoot unless the air temperature is above about 5°C (Taylor, 1967).

Some 60% of P stored in one-year-old *Pinus densiflora* (red pine of Japan) and *Larix leptolepis* (Japanese larch) was utilized in new shoot growth the following year (Mutoh, 1972). Two-year-old leafless *L. leptolepis* contained 17.7 mg of P and absorbed a further 3.8 mg until mid-April. During this time 11.2 mg of P were used in new shoot growth and 2.4 mg for new root growth. Thus 9.8 mg (72%) of P were obtained from storage within the plant for new growth. Roots of these young deciduous trees were a primary storage site for P.

(2) Bark

The bark, and to a lesser extent the wood, of young apple shoots can store soluble N compounds and proteins, which are hydrolysed before translocation of simpler N compounds to new growth in spring (Tromp and Ovaa, 1971, 1973). In forest trees, arginine accumulates in *Populus gelrica* (poplar) bark and wood from cessation of shoot growth, in August, and decreases about a month before bud break in May (Sagisaka, 1974). This may not all go to new shoot growth because glutamine and glutamate increase as arginine decreases, and there is an overall increase in bark and xylem amino acid concentrations until June, after which the concentrations drop to a low level. This early summer increase in total amino acids could have been due to hydrolysis of proteins, as in *Populus balsamifera* (balsam poplar) Höllwarth, 1976). Marked increase in protein N occurs between late summer and winter in the bark of many trees (Parker, 1958) and apparently at least some is re-hydrolysed the following spring.

The importance of various storage sites can be partly judged from a balance sheet of N in dormant and flushed apple trees (Table II). Only net gains and losses in various parts of the tree can be determined and one can not be certain of the precise movement of N because the trees absorbed 164 mg N between February and May. Reductions of total N were roughly equal in bark, wood and roots, and amounted to 119 mg which accounted for 42% of the N present in leaves in May. A relatively large reduction of 52 mg of insoluble N, presumably mainly protein, occured in bark. A proportion of this may have remained as soluble N because the bark showed an increase of 14 mg soluble N. A noticeable reduction in arginine, equivalent to 27 mg N, occurred in wood.

Bark may be a storage site for other nutrients besides N. Close to a quarter of the total P and K in 40-year *Populus tremuloides* was in bole bark (Alban *et al.*, 1978). Bark seems to contain a relatively lower proportion of nutrients in conifers and only 16% of total tree P and 20% of total tree K was in bole bark of 36-year *Pseudotsuga menziesii*) (Cole *et al.*, 1967). Since these figures relate only to bole bark, the actual proportion of nutrients in bark of the above-ground parts of the tree can be revised upwards by about 10%. The proportion of nutrients contained by bark becomes even larger if root bark is included. In old growth *P. menziesii* root bark has 3–6 times higher concentrations of P than root wood, but bark K concentrations are only about 1.5 times greater than wood concentrations (Santantonio *et al.*, 1977).

(3) Branches and wood

Bark is seldom separated from wood of branches in studies of nutrient

Table II. Distribution of dry matter, total N and N fractions in young apple trees.[a]

Tree component	Dry weight (g)	Nitrogen in various fractions (mg N)				
		Total	Arginine	Asparagine	Other	Insoluble
			February			
Bark	12.7	197	19	12	5	161
Wood	32.9	235	92	22	1	120
Roots	11.6	226	61	40	3	122
Total tree	57.2	658	172	74	9	403
			May			
Leaves	7.9	283	3	8	7	265
Bark	12.5	159	20	24	6	109
Wood	29.1	196	65	27	6	98
Roots	8.6	184	53	42	3	86
Total tree	58.1	822	141	101	22	558
			Differences May–February			
Bark	−0.2	−38	1	12	1	−52
Wood	−3.8	−39	−27	5	5	−22
Roots	−3.0	−42	−8	2	0	−36

[a]Averages for urea and KNO_3 fertilized trees sampled in mid-February and mid-May (after Cooper *et al.*, 1976).

distribution so that comparison of the role of bark *vs* branches as nutrient storage sites cannot be made. However several observations show that N concentrations in twigs and young branches are relatively high, and it is possible that they contain local reserves for bud expansion and leaf growth. Nitrogen percentage in twigs increased as much as foliage N percentage after fertilization of *Pinus elliotii*, and arginine in twigs increased about 2.5 times as much (Barnes and Bengtson, 1968). Similarly, in two-year old *Pseudotsuga menziesii* receiving N fertilizers, the increase in concentration of guanidino compounds was as high in twigs as in foliage (van den Driessche and Webber, 1975). Nitrogen from fertilizer labelled with N^{15} accumulated more in twigs of one- and two-year-old shoots than in foliage of *Pinus sylvestris* at the end of the growing season (Nömmik, 1966), suggesting an over winter storage function for twigs.

Branches seldom exceed a fifth of the whole tree biomass (Table I), and twigs comprise a much smaller part. Thus the fraction of the tree's total nutrient in branches, and particularly twigs, is small. However, current

needles and the annual flush of leaves in broad-leaf trees contain quantities of nutrients that are comparable to the quantities found in twigs. Consequently, twigs and branches would be capable of supplying important amounts of nutrients for a new leaf growth. In a 150-year forest consisting predominantly of *Quercus alba* (white oak), twigs composed only 3% of the biomass, and contained 5% of the N, K and Ca, and 3% of the P (Rolfe *et al.*, 1978). However the foliage only contained two to three times these amounts (Table I). In a 450-year *Pseudotsuga menziesii*, twigs less than 1 cm in diameter contained 252 g N, 50 g P, 323 g K and 854 g Ca, whereas current needles contained 180 g N, 34 g P, 215 g K and 87 g Ca (Overton *et al.*, 1973). Of course, the total nutrient content of all needles exceeded the nutrient content of twigs because there were several age classes of needles present.

Many observations suggest that spring shoot development can be sustained for some time by the utilization of internal P reserves, which like N, appear to be stored in both roots and stems. Expanding shoots of three-year-old *Pseudotsuga menziesii* gained 0.17 mg P, whereas one-year-old shoots lost 0.24 mg P, following bud burst (Krueger, 1967). Clearly all the P required by new shoots during spring could have been supplied from old shoots.

Phosphorus compounds of foliage and twigs include nucleic acids, inorganic P, ester P and lipid P. Phosphorus is translocated in the inorganic form, and nucleic acids and lipid P predominate in temperate trees during winter. Buds of *Betula papyrifera* (white birch) contained 30–38% nucleic acid P, but in mature and senescing leaves 55% inorganic P was measured as mobilization for retranslocation occurred (Chapin and Kedrowski, 1982). In these studies in young branches nucleic acid P was always most abundant, but ester P increased to 27% of P in winter. Lipid P increased in autumn and winter in twigs of deciduous species and leaves of *Picea mariana* (black spruce).

The probable importance of stem wood as a nutrient storage site in several Australian tree species has been discussed by Bowen (1980). Concentrations of P, K and, to a lesser extent, Ca are lower in heartwood than sapwood suggesting that a proportion of sapwood nutrients are reutilized as heartwood is formed. There is a similar decrease in P and K concentrations between sapwood and heartwood in pine (Table III). It might be supposed that N, as well as P and K, would be redistributed from wood being converted to heartwood, as happens in ageing and senescing leaves. In fact N does not seem to be redistributed to any extent, although there is some evidence for it in *Pseudotsuga menziesii* (Table IV). Sapwood may contain a large proportion of a tree's nutrient capital. For example, sapwood in 66-year-old *Eucalyptus obliqua* (messmate stringybark) contains 33% of all P and 18% of all K in above-ground portions of the tree, and in 27-year-old

E. grandis (flooded gum) corresponding values are 23% for P and 29% for K (Turner, 1981).

Table III. Concentration of nutrients in sapwood and heartwood of pines and eucalypts.

Species	Age	Type of wood	Concentration of nutrient (ppm) N	P	K	Ca
Pinus sylvestris[a]	64 yr	Sap	680–1060	44–132	260–740	280–830
		Heart	640–700	9–24	130–180	540–730
Pinus nigra[a]	48 yr	Sap	680–950	37–98	290–900	300–850
		Heart	720–910	20–27	180–400	660–860
Pinus radiata[b]	mature	Sap	800	65	690	520
		Heart	900	10	300	750
Eucalyptus grandis[b]	mature	Sap	2,900	130	1,250	650
		Heart	2,400	5	200	750
Eucalyptus muellerana[b]	mature	Sap	3,100	140	850	1,110
		Heart	2,100	15	10	320

[a]Wright and Will, 1958.
[b]Turner, 1981.

(4) Foliage

The quantities of nutrients contained in foliage may amount to more than 30% of the total nutrient in the tree (Table I). Redistribution of nutrients from foliage to reduce the potential loss associated with shedding of leaves appears to have evolved in many trees and will be discussed below (IV, B; IV, C). In two species of comparable biomass the evergreen *P. menziesii* (above ground biomass 65 t ha^{-1}) foliage contained close to 50% of the N, P, and K, and 40% of the Ca in the tree (Webber, 1977). The deciduous *Betula verrucosa* (above ground biomass 62 t ha^{-1}) foliage contained 25% of the N, 21% of the P, 36% of the K and 14% of the Ca in the tree (Ovington and Madgwick, 1959b). Thus the evergreen foliage is proportionally a larger reserve of nutrients than the deciduous foliage, and because perhaps only a fifth of the evergreen foliage is shed each year the potential annual loss in non-translocated nutrients is less.

B. Nitrogen Storage Forms

Proteins are probably the most important N reserves in trees. They contain 75–80% of the N in bark and 50–60% of the N in wood of young apple trees

(O'Kennedy *et al.*, 1975), and about 60% of all the N in entire young trees (Table II, insoluble N compounds are primarily proteins). A study of *Larix laricina* (American larch), *Picea mariana*, *Betula papyrifera* and *Alnus crispa* in Alaska showed that throughout the year protein comprised more than 70% of the total N in foliage and young branches (Chapin and Kedrowski, 1983). In spring the N concentration of apple bark decreases (e.g. Table II) mainly due to hydrolysis of proteins which account for 60–70% of the N exported (Tromp and Ovaa, 1973). These proteins were hydrolysed almost completely into arginine and asparagine, with arginine comprising as much as 23% of the amino acids released in bark of well-fertilized apple trees. However, in trees receiving moderate fertilization, arginine accounts for only about 11% of the N released as amino acids from shoot protein (O'Kennedy and Titus, 1979).

Soluble N compounds, primarily amino acids, are important storage forms in fruit trees (Taylor, 1967) and in forest trees (Barnes and Bengston, 1968). Arginine is one of the most abundant amino acids in tree tissues and is generally believed to be important as a N storage substance. It has a relatively low C:N ratio and contains four organic N in the form of amino and guanidyl groups which are readily converted to other amino acids and nitrogenous compounds.

Following N fertilization, the level of asparagine in apple tissue usually rises rapidly indicating N is first incorporated into this amino acid. Afterwards the arginine level increases and asparagine decreases (Tromp and Ovaa, 1979). The arginine level in apple trees can be increased at almost any time of the year by N fertilization (Hill-Cottingham and Cooper, 1970), and it is probably important to remember that fruit trees are normally well supplied with N whereas forest trees seldom are. Consequently large accumulations of N storage compounds, and in particular arginine, may not be encountered in forest trees. However, where forest trees are fertilized, the concentrations of arginine and other soluble N compounds increase (Barnes and Bengston, 1968; van den Driessche and Webber, 1977 a, b).

Arginine may function as an N storage compound when N is abundant because its low C:N ratio creates minimal demand for photosynthate. It is usually converted into other amino acids in actively growing tissue. In *Picea glauca* saplings, glutamine, glutamic acid and proline levels increased as concentration of arginine in buds decreased during flushing in May. However, arginine again became abundant, together with alanine, serine and aspartic and gamma-amino butyric acids, when shoot extension was complete (Durzan, 1968).

Inadequate supply of another nutrient may result in relative abundance of N and, for example, insufficient S has been found to result in accumulation of arginine, which contains no S (Turner and Lambert, 1978). Organic S and

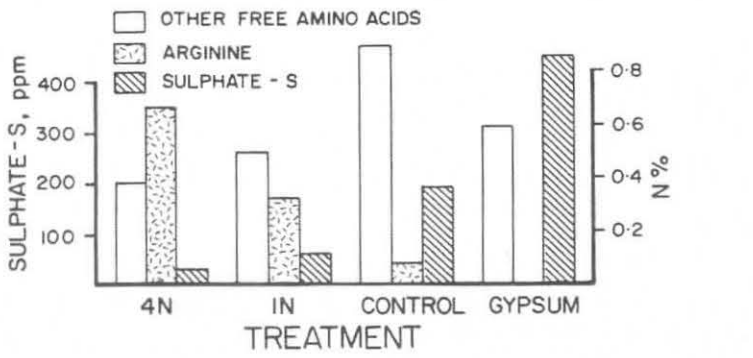

Fig. 1. Effect of N and gypsum ($CaSO_4$) fertilizers on amino acid and sulphate-S levels in foliage of 4-year *Pinus radiata* (from Turner and Lambert, 1978).

total N normally occur in foliage of pines, *Pseudotsuga menziesii* and *Eucalyptus* spp. in the same ratio (0.030) as that of S:N in foliar proteins (Turner and Lambert, 1979). Addition of ammonium nitrate to a four-year-old *Pinus radiata* plantation, which already had an adequate foliar N level, induced a large increase in arginine level and a reduction in levels of other free amino acids (Fig. 1.). On the other hand fertilization with gypsum reduced levels of arginine and other free amino acids.

A third group of compounds containing significant amounts of N are nucleic acids. In two conifers and two hardwoods from the Alaskan taiga, foliar and branch tissues contained more N in nucleic acids than in free amino acids for much of the year (Chapin and Kedrowski, 1983) (e.g. Fig. 2—*Betula papyrifera*). Nucleic acids comprised 20% of bud N and about 8–11% of leaf N in *Betula papyriferea* and about 4–9% of leaf N in *Picea mariana*.

Despite the possible effects of the form of external N supply on metabolism and storage (e.g. Cooper *et al.*, 1976) a general relationship between form of external N supply and internal metabolism and storage has yet to be established. Analyses have usually been conducted on tissues which can show different responses. For example, root tissues of apple accumulated more arginine on a nitrate source than on an ammonium source, but new spring growth of the same trees accumulated more arginine on the ammonium source (Tromp and Ovaa, 1979). The time chosen for analysis may affect the apparent response, and different N sources may have a number of incidental effects such as altering pH or changing the availability of other nutrients. Depending on environmental conditions, these incidental effects might influence internal metabolism and storage. This may explain why the suggestion has been made that reduced forms of N promote accumulation of

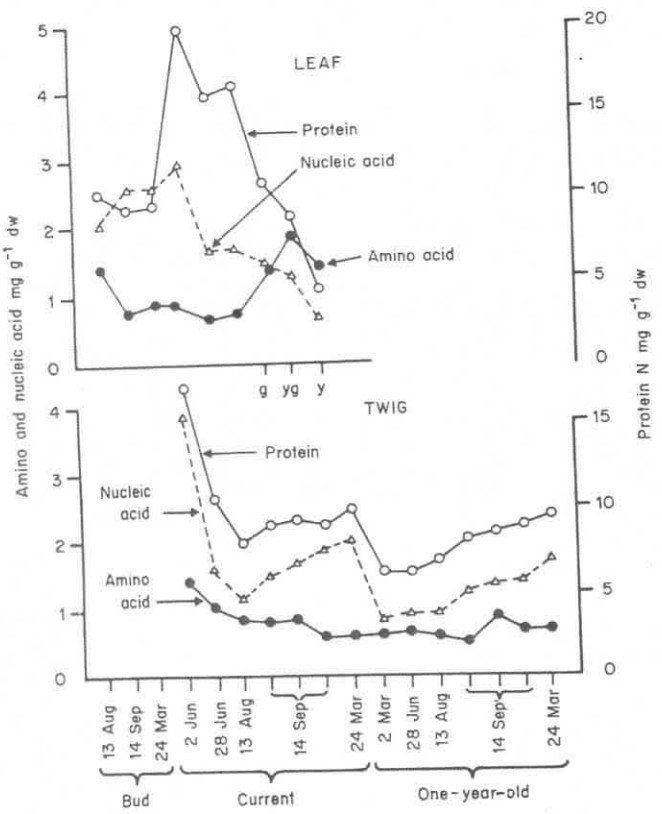

Fig. 2. Change in concentrations of proteins, amino acids and nucleic acids in leaves and twigs of *Betula papyrifera* with time. Letters g, yg and y refer to leaf colours green, yellow green and yellow respectively (from Chapin and Kedrowski, 1983).

arginine in pine shoots (Barnes and Bengston, 1968) yet 17-month-old *Pinus banksiana* contained more arginine when fed on nitrate-N than when fed on ammonium-N (Durzan and Steward, 1967).

IV. TRANSLOCATION

A. Translocation Within the Tree

(1) Xylem transport

After uptake, long distance transport of mineral nutrients takes place primarily in the xylem where they are passively carried in the transpiration

stream (Lüttge and Higinbotham, 1979). About a third of the total solids in the xylem sap are inorganic ions: K^+, Ca^{2+}, Mg^{2+}, Na^+, $PH_2PO_4^-$, Cl^- and SO_4^{2-} being the major ones (Pate, 1976). Both P and S may also be present in organic compounds.

Any NH_4-N which is absorbed, as in conifers, is metabolized in roots, but nitrate may be translocated in xylem sap (Hill-Cottingham and Lloyd-Jones, 1979). Nitrate is not abundant in xylem sap of apple or *Pinus*, but occurs in xylem sap of *Citrus* (Kato, 1981). Organic N compounds, particularly amino acids, are usually major components of xylem sap (Pate, 1976). In apple, arginine, asparagine and glutamine comprise some 90% of the amino acids present in xylem sap, but arginine predominates in March and asparagine in May (Hill-Cottingham and Lloyd-Jones, 1979). The high concentration of arginine in xylem sap in early spring may represent mobilization of N from within the tree, whereas newly absorbed N is translocated primarily as asparagine (Tromp and Ovaa, 1976). This is supported by the observation that the amino acids predominantly labelled in xylem sap of citrus-fed ^{15}N were asparagine and glutamine, although arginine accounted for 48% of the N in the sap (Kato, 1981).

The composition of xylem sap is not constant as it flows through the tree and amino acids may be differentially accumulated and metabolized in xylem tissue (Hill-Cottingham and Lloyd-Jones, 1979).

(2) Phloem transport

Phloem sap is more concentrated than xylem sap and 80–90% of the solids in the sap are carbohydrates, with sucrose often most abundant (Pate, 1976). The carbohydrates produced in photosynthesis are primarily translocated downwards in phloem, but transport is bidirectional because young leaves and fruit are supplied with carbohydrates through the phloem. Low molecular weight N compounds, mainly amino acids and amides are also readily mobile in phloem (Ziegler, 1975). Analysis of phloem sap of 23 hardwoods from the northern temperate zone shows that serine, asparagine, glutamine and valine are quantitively most important and that arginine and glycine only occur in trace amounts. A bark ringing experiment conducted on young apple trees showed that translocation of stored N compounds occurred upward through the phloem in spring (Tromp and Ovaa, 1971).

Mineral elements have different mobilities in the phloem, and K appears to be the predominant cation present in northern temperate hardwood sap. Concentrations of K in phloem sap of such species were found to range from 0.4 to 20 mg ml^{-1}, concentrations of Mg from 0.05 to 2.2 mg ml^{-1} and concentrations of Ca from 0 to 0.2 mg ml^{-1} (Zeigler, 1975). Other elements, besides K, Mg and N, which are readily mobile in phloem include P and S.

Retranslocation from senescing tissue take place through the phloem as indicated by the increase in level of amino compounds in phloem of deciduous species at leaf senescence (Pate, 1976).

B. Translocation Between Trees

Natural grafting between roots of forest trees is a wide-spread phenomenon (Bormann, 1961), and may be a feature which influences response of forest crops to nutritional factors. Grafting normally occurs between trees of the same species and may reach a high frequency in old stands so that up to 80% of the trees in a stand are connected to other trees through their root systems. Groups of trees are frequently interconnected by a number of grafts (Bormann, 1966; Eis, 1972). Considerable evidence for translocation from tree to tree through root grafts is based on studies with dyes and radio-isotopes, but, with the exception of ^{32}P, none of the substances used were nutrient elements. On the other hand they provide evidence of a xylem stream in which mineral nutrients are probably translocated. Movement of ^{32}P has been demonstrated from both suppressed to dominant trees and vice versa (Bormann, 1966; Kuntz and Riker, 1956). Study of root diameters proximal and distal to grafts suggested that net transfer of photosynthate between roots was greater to the root which was grafted further from its origin at the base of the tree (Armson and van den Driessche, 1959). Direction of mineral nutrient movement could also be influenced by position of the graft relative to the trees which are joined, and to polarity of the graft.

No estimates of quantities of nutrients moving through root grafts seem to have been made, and it is uncertain, for example, to what extent nutrient reserves in stumps and root systems of trees removed by thinning can be used by crop trees grafted to them. There is also evidence that small amounts of nutrients can move between tree root systems in the absence of grafts (Woods and Brock, 1964; Hansen and Dickson, 1979). Mycorrhizal hyphae are suggested as one pathway for this to occur under forest conditions.

V. RETRANSLOCATION

Retranslocation of nutrients is thought to take place from mature tissue to actively growing regions more extensively under conditions of nutrient stress (Williams, 1955). In studies by Florence and Chuong (1974), current foliage of *P. radiata* growing on sites of different fertility showed little difference in N

or P concentration, but older needles of trees on the most infertile soils showed lower concentrations, particularly of P, than trees on more fertile soils, suggesting more N and P retranslocation on infertile soil. In lowland rainforests on the Ivory Coast, Brazil and Guatemala, little N is withdrawn from foliage before it is shed (Grubb, 1977). This could be because abundant mineralization of N takes place in these soils. In small stature (12 m tall) upper montane tropical rainforest in Jamaica, some 50% of the N and 65% of the P are removed from the foliage prior to leaf fall, but in tall stature lower montane tropical rainforest (33 m tall) in New Guinea equivalent figures for N were 14% and for P 29%.

Nutrient stress may also be induced by conditions limiting uptake from the soil; in drought conditions Will (1968) found a reduction of Mg uptake in *Pinus radiata*, which led to Mg deficiency in older needles as Mg was retranslocated to new growth.

The quantities of nutrients retranslocated may be considerable and can occur from many tissues with age. Retranslocation was estimated to supply 41% of the N, 45% of the P and 26% of the K required annually by 73-year-old *Pseudotsuga menziesii* (Table IV). Switzer and Nelson (1972) estimated that 39% of N, 60% of P, 22% of K, 24% of Mg and 22% of S required by 20-year-old *Pinus taeda* (loblolly pine) trees is obtained by retranslocation. It is not clear, however, to what extent various species differ in their inherent ability to retranslocate nutrients and to what extent retranslocation is affected by nutrient stress. At least in the American Pacific Northwest, conifers are able to meet more of their nutrient requirement from redistribution than are hardwoods, giving the conifers a competitive advantage (Waring and Franklin, 1979). Research also indicates that a major reason for the success of species such as *Pinus nigra* var. *maritima* (Corsican pine) on soils of low nutrient status is their efficient external and internal cycling of nutrients (Miller *et al.*, 1979). With half or more of the requirements for some nutrients being met by internal cycling, differences in this process between species and provenances are likely to become increasingly important in silviculture and tree breeding.

A. Measuring Retranslocation

Probably the most widely studied retranslocation is between foliage and shoot. In conifers there may be steady nutrient removal from foliage over months or years, but normally the main removal in deciduous species occurs during the last three or four weeks before abscission. Nutrients removed from the leaves are translocated into the stems or younger foliage. The redistribu-

Table IV. Distribution of dry matter and four macronutrients together with estimated annual retranslocation of nutrients in 73-year-old *Pseudotsuga menziesii* trees.[a]

Components	Dry Matter ($t\,ha^{-1}$)	Nutrient content ($kg\,ha^{-1}$) N	P	K	Ca
Foliage					
Current Content	2.3	28	3.9	20	12
Total Content	10.7	114	24.2	76	115
Retranslocation		9.8	1.7	4.6	−26.8[b]
Branches					
Current Content	0.3	3	0.2	2	1
Total Content	15.4	62	5.8	61	72
Retranslocation		1.3	0.1	0.4	−0.2
Bole Wood					
Current Content	2.5	4	0.3	3	1
Total Content	236.9	107	12.0	153	97
Retranslocation		3.3	0.2	1.4	0.2
Bark					
Total Content	30.4	67	12.5	64	149
Whole Tree					
Total Content (above ground)	293.5	350	54.5	354	433
Retranslocation		14.4	2.0	6.4	−26.8

[a]After Turner (1975).
[b]Negative value represents accumulation in old tissue.

tion is considered part of the internal cycle or the biochemical cycle (Switzer and Nelson, 1972).

Reduction in leaf nutrient concentration does not necessarily represent export of nutrient from the leaf. Although this assumption is usually safe (Grubb, 1977; Attiwill *et al.*, 1978) during the later part of a leaf's life when dry weight increment is small or non-existent, it is undoubtedly an unsafe assumption during the early life of the leaf. For example until August in maples and oaks in eastern North America (Mitchell, 1936) and until June in Douglas fir (Krueger, 1967) and in Australian sclerophyllous plants, which may increase their dry matter content per unit of leaf area by 15–40% over two years prior to senescence (Beadle, 1968).

Another difficulty in determining how much nutrient is recycled internally can be caused by rain leaching nutrients from leaves (Switzer and Nelson, 1972). However it is not sufficient to merely deduct the quantity of nutrient in leachate from the apparent withdrawal because throughfall rain contains

additional nutrients picked up from dust and aerosols (see Chapter 3). Possibly gaseous losses of N also occur from forest foliage (Luxmore *et al.*, 1981) in the same way that ammonia is released from senescing corn (*Zea mays*) foliage (Farquhar *et al.*, 1979). In a study with *Pinus nigra* var. *maritima* in Scotland (rainfall 600 mm per annum) contributions from dust and aerosols were measured which suggested that there were no losses of N and P from needles due to leaching, but 89% Na, 48% of Mg, 44% of K and 8% of Ca reaching the forest floor was leached from the foliage (Miller *et al.*, 1976). Leaching of nutrients from foliage is probably an important feature in tropical rain forests (Grubb, 1977).

B. Retranslocation from Hardwood Foliage

Withdrawal of N and K from foliage before abscission is common, and this is reflected in the lower nutrient concentration in old leaves compared to young leaves (Table V). Retranslocation of Mg, Fe and S sometimes occurs, but Ca and Na are not retranslocated. Retranslocation of N, P, and K took place in *Quercus coccinea* (scarlet oak) from mid-September until leaf abscission (Fig. 3). About 50% of the N, 80% of the P and 55% of the K was withdrawn from the leaves by the time abscission occurred. After allowing for leaching, retranslocation of nutrients from foliage of *Q. prinus* (chestnut oak) at leaf fall

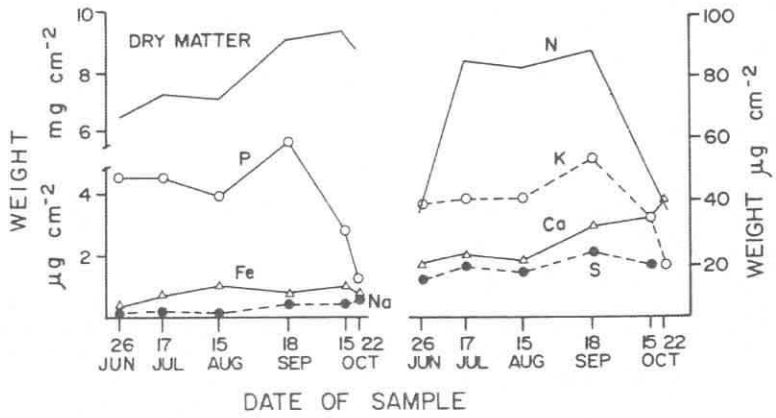

Fig. 3. Change in weight of dry matter and mineral nutrients on a leaf area basis through the growing season for *Quercus coccinea* (from Woodwell, 1974).

was computed as 78% of the N, 54% of the P, 53% of the K and 8% of the Ca present in mid-August (Ostman and Weaver, 1979).

In *Fagus sylvatica* (beech) some 45% of the N and K is withdrawn between late September and leaf fall (Olsen, 1948). Although there is no indication of P withdrawal from leaves of *F. sylvatica*, and Attiwill *et al.* (1978) cite Russian evidence for lack of P withdrawal from oak foliage, P is withdrawn in many other hardwood species prior to abscission (Table V). As much as 70–80% of

Table V. Changes in leaf nutrient concentrations between young and old leaves.

		Nutrient concentration										
		leaf dry weight (%)						dry leaf (ppm)				
Species		N	P	K	Ca	Mg	S	Fe	Mn	Cu	Zn	Na
Fagus sylvatica[b]	Y[a]		0.15	0.74	0.55	0.13		105	236	4.2	23	1500
	O		0.26	0.50	0.51	0.14		120	212	3.3	25	2400
Aesculus	Y		0.13	0.87	0.86	0.22		294	128	4.6	12	1100
hippocastanum[b]	O		0.08	0.46	1.05	0.22		353	115	3.1	20	1900
Betula	Y	2.47	0.19	1.02	0.97	0.27	0.17					
alleghaniensis[c]	O	1.12	0.11	0.42	0.98	0.18	0.08					
Eucalyptus	Y	0.84	0.04	0.57	0.58					2.9	5.6	
marginata[d]	O	0.30	0.01	0.26	0.74					2.5	3.0	
E. calophylla[d]	Y	0.91	0.05	1.08	0.66					2.8	9.4	
	O	0.30	0.01	0.66	0.85					2.8	6.5	

[a]Y = young leaf; O = old leaf; [b]Guha and Mitchell, 1966; [c]Hoyle, 1965; [d]O'Connell *et al.*, 1978.

P may be removed from leaves of some *Eucalyptus* species before leaf fall (Attiwill *et al.*, 1978). Interestingly, significant removal of N and P back into branches took place from partly damaged *E. marginata* (jarrah) leaves at the top of the crown, following controlled burning (Glossop *et al.*, 1980). This was thought to be a nutritional adaptation in a species where fire is a natural feature of the environment.

C. Retranslocation from Conifer Foliage

Nutrient mobilities in conifer foliage are the same as in hardwood foliage, except that perhaps there is more evidence for Mg retranslocation (Will, 1968). Although sampling of different ages of needles at the same time of year

suggests that there is little change in nutrient concentration until shortly before abscission (Table IV), it is now clear that translocation out of needles and resupply can occur during a single season.

Fife and Nambiar (1982) showed that substantial amounts of nutrients can be withdrawn from young *Pinus radiata* needles to support seasonal growth of new shoots. They estimated that on a tree basis 86, 48 and 39% of P, N and K respectively, in summer shoots could have come from retranslocation from 4–5 month-old needles formed during the preceding spring. Later, recovery to spring needle nutrient levels coincided with autumn rain. Some seasonal fluctuation of needle N content also appears to occur in *P. rigida* (pitch pine) (Woodwell, 1974). Maxima of about 30 and 33 g cm^{-1} of needle in July and October of the first year contrasted with minima of about 20 g cm^{-1} in August of both first and second years. Needle P content decreased steadily from about 2 g cm^{-1} during the second year. However larger decreases, amounting to about 26 g N cm^{-1}, and 1 g P cm^{-1}, occurred in late September just before abscission.

In *Picea mariana* there is little evidence for nutrient retranslocation prior to abscission, although the proportions of different N and P fractions changed with season (Chapin and Kedrowski, 1983).

The quantities of nutrients retranslocated from needles shortly before abscission are considerable (Table VI). Wells and Metz (1963) estimated

Table VI. Annual change in needle weight and nutrient content in *Pinus sylvestris*.[a]

Needle age, years	Dry weight (g per 1000 needles)	Nutrient content (mg per1000 needles) N	P	K	Ca
1	6.04	90	9.5	42	14
2	6.87	91	9.5	42	20
3	7.22	95	9.7	40	22
4	8.00	104	10.7	40	30
Yellowed	6.67	33	2.0	8	35
Change at yellowing, %	− 17	− 69	− 81	− 80	+ 18

[a]From Mälkönen, 1974.

withdrawal of nutrients from needles of *Pinus taeda* in October by comparing content of green and yellow needle fascicles, and found that amounts removed were: N, 52%; P, 47%; K, 62%; Mg, 18%.

VI. RELATIONSHIPS BETWEEN MINERAL NUTRIENTS AND STRESS

A. Drought Stress

High N levels have generally been found detrimental to growth and survival under drought conditions, intermediate N levels have either been beneficial or had no effect and drought has had least effect on growth of trees at low N levels (Pharis and Kramer, 1964). Effects of N supply on seedling drought resistance can often be explained in terms of growth. An increased N supply decreased drought resistance (as measured by time till death) in *P. resinosa*, but it also increased seedling size and decreased root/shoot ratio (Shirley and Meuli, 1939). In drought tests of 3 to 8 days, the relative size of transpiring shoots was probably a determining factor.

Increased relative leaf mass of six-week-old *P. contorta* seedlings, obtained by an increased nitrate supply, reduced recovery from a two-week drought exposure by 39% (Etter, 1969). In a second experiment drought avoidance by smaller seedling was eliminated by allowing the rooting medium to dry uniformly to 2–3% moisture; an adverse effect of high nitrate supply was still discernable, but recovery was only reduced by 13%. This could indicate some feature of N metabolism affecting drought resistance. However, the faster recovery of 8-month *P. taeda* seedlings containing 2.0% foliar N compared with seedlings containing 1.3% foliar N, which were both exposed to a uniform drought stress (Pharis and Kramer, 1964), was probably related to the greater N reserves available for growth, particularly of roots, when drought stress ceased.

High levels of foliar K are associated with reduced transpiration rates in several tree species (Tsutsumi, 1959; Christersson, 1973; Glatzel, 1976; Bradbury and Malcom, 1977). The rapid reduction in transpiration rate sometimes resulting from K fertilizer application suggests that K acts physiologically (Bradbury and Malcolm, 1977). This is likely to be due to a regulatory effect on stomatal movement. The effect of K is illustrated by *Picea sitchensis* seedlings for which water use efficiency was calculated over a 5-week period and expressed as g water used per g new shoot dry weight (Bradbury and Malcolm, 1977). Seedlings with 1.0 and 1.9% foliar K used 188 and 156 g water g^{-1}, respectively. Transpiration rates may also be reduced by low foliar K (0.24%) compared with intermediate foliar K (1.2–1.4%) levels (Christersson, 1976). In this lower range increased K concentration increased drought survival of *Pinus sylvestris*, but not *Picea abies*, suggesting improved drought hardiness in the pine.

Dormant seedlings, which are more drought resistant than actively

growing seedlings, show much less effect of K level on transpiration rate than actively growing seedlings (Christersson, 1973; Bradbury and Malcolm, 1977). However, adequate K nutrition can increase drought avoidance of young dormant *Pseudotsuga menziesii* under frozen soil conditions (Larsen, 1978).

B. Cold Stress

Influences of mineral nutrition on cold hardiness has long been studied (Levitt, 1956; Alden and Hermann, 1971), but underlying principles are not well established, particularly in regard to trees (Aronsson, 1980). Sometimes effects are due to changes in the growth pattern caused by nutrition; high levels of N in nursery stock can result in frost damage, but this is because dormancy is delayed, and the same effect can be achieved with high P fertilization (Malcolm and Freezaillah, 1975). Similarly, high levels of N supply to *Picea abies* seedlings have resulted in earlier flushing the following year and corresponding decreases in cold hardiness (Pümpel *et al.*, 1975).

Claims for a particular role of nutrition in development of cold hardiness have to be examined with caution because some reports relate to plants probably not capable of any significant frost hardening (Beattie and Flint, 1973). Also, one occasionally cited report on the effect of K-induced hardiness in conifers (Kopitke, 1941) measured only the freezing point, osmotic pressure and simple sugar content of expressed sap, but not the cold hardiness of the seedlings. However N and K, applied to nursery seed beds so late in the season that growth was unaffected, did influence frost susceptibility of both *P. sitchensis* and *Tusga heterophylla* (western hemlock) (Benzian, 1966); N treatment reduced December frost damage by about half or more, and K virtually eliminated it. Similarly, significant reduction of winter frost damage to 10-year-old *Pinus sylvestris* trees and a Finnish provenance of *Picea abies* have resulted from K and P fertilizer, but not N fertilizer, applied at planting (Koskela, 1970). The effect of K appeared greater than P, but when applied together the effects of P and K were additive.

Maximum cold hardiness of shoots of 16–17-year *Pinus sylvestris* occurred at a needle N concentration between 1.3 and 1.8% in studies by Aronsson (1980). In general, more freezing damage was sustained by shoots with N concentrations outside this range. It was suggested that the difference in damage among trees of high N status was related to their boron nutrition since needles of some trees showed concentrations as low as 1.5 ppm. In Norway, shoot damage to *P. sylvestris*, *P. contorta*, *Picea abies* and *Betula pubescens*, thought to be caused by frost, was associated with low levels of

boron (Braekke, 1979). Low levels were detectable in the previous year's needles of the conifers, but seldom fell below the 3 ppm acute deficiency level. It was concluded that boron levels should exceed 8–10 ppm in conifer foliage and 14–16 ppm in birch foliage to avoid frost injury. Boron deficiency has also been reported to decrease frost resistance in *Eucalyptus grandis* (Cooling, 1967), but no effect of boron on cold hardiness of *Pseudotsuga menziesii* was detected with tissue concentrations ranging from 27–167 ppm boron (Larsen, 1976), tending to confirm that boron has little effect on cold hardiness above a relatively low level.

Timmis (1974) found that, after a hardening period, young *P. menziesii* seedlings with an internal K:N ratio of about 0.6 were hardier than those with a ratio of 1.3. There now seemes good evidence that high levels of K do not directly increase cold hardiness in trees (Christersson, 1976; Aronsson, 1980). It seems very likely that improved drought resistance conferred by K has been mistaken in the past for increased cold hardiness under conditions where water stress is associated with low temperatures in the field.

C. Disease

Mineral nutrition can influence susceptibility of trees to fungal disease (Dimitri, 1977) and to insect attack (Stark, 1965; Baule and Fricker, 1970). However the effects of particular nutrients often seem to depend on environmental conditions. For example, incidence of fusiform rust (*Cronartium fusiforme*) on *Pinus elliotii* was increased by additions of N and P fertilizers on some poor and moderatly drained sites, but not on any well-drained sites (Hollis *et al.*, 1975). A significant increase in rust infection of *P. elliottii* seedlings also resulted from an increased level of P fertilization under green-house conditions (Schmidt *et al.*, 1972).

An adequate supply of all nutrients is often found to reduce incidence of disease, as, for example, the reduction of *Lophodermium pinastri* infection on *Pinus sylvestris* (Zöttl and Jung, 1964) due to addition of N, P, K and Mg. There is other evidence that improved nutrition in pine, resulting from fertilization can reduce incidence of this needle cast disease (Baule and Fricker, 1970). Similar balanced nutrition was shown to reduce *Marsonina* infection of *Populus* as well (Garbaye and Pinon, 1973).

However it has been shown that attack of *Marsonina* leaf disease is much more prevalent on foliage of low K concentration (less than 1.3%), with leaves of more than 2.0% suffering little attack (van der Meiden, 1959). Reduction in resistance of poplar leaves to *Melampsora* infection (Suzuki and Chiba, 1973), and of *Quercus sessiliflora* leaves to mildew (*Microsphaera*

alphitoides) attack (Penningsfeld, 1964) have both been attributed to inadequate K nutrition. Severity of other fungal leaf diseases is also apparently reduced when K supply is adequate (Baule and Fricker, 1970). Die back and associated fungal disease of *Pinus radiata* have been attributed to both low S and low B (Lambert and Turner, 1977). These deficiencies appear to predispose the trees to growth disorders and often to infection by *Diploda pinea*. *P. radiata* seedlings grown for four months in culture solutions at varying sulphate levels showed differences in resistance to infection after surface application of *Diplodia pinea* spores and hyphae (Turner and Lambert, 1978). Severe infection was complete within a week in S deficient (foliar SO_4-S 20–35 ppm) seedlings, but it took at least two weeks for infection to occur in seedlings with adequate S.

Wood and bark borers are primarily controlled by resin and bark sap pressure and fertilization probably tends to increase production and pressure of these substances (Stark, 1965). Improvements of N and Ca nutrition of pine species also reduced damage by a number of insects, primarily by increasing larval mortality. Foliar applications of different forms of N fertilizer to *Abies grandis* (grand fir) affects survival of the balsam wooly aphid pest (*Adelges piceae*) (Carrow and Graham, 1968). Ammonium nitrate reduces the population growth of aphid, but urea and calcium nitrate promote aphid population growth. Analysis of *A. grandis* bark, where the aphid most commonly feeds, showed that ammonium nitrate increased arginine levels in the bark more than the other fertilizers, and that neither phenylalanine nor asparagine were present in bark of ammonium-treated trees (Carrow and Betts, 1973). The free amino acid composition of *A. grandis* foliage was also influenced by N nutrition, although not in the same way as bark (Carrow 1973). Thus mineral nutrition substantially affects physiology of trees and it is assumed that this, in turn, influences insect growth and development. Baule and Fricker (1970) summarized a review of mineral nutrient effects of insect diseases of trees by saying that K generally reduced attacks by sucking insects, but N intensified attacks. However, N, NPK and Ca treatments tended to reduce attack by eating insects. It would be interesting to know whether the effect of K in reducing fungal leaf disease, and perhaps sucking insect attacks, is related to its effect in improving water economy of trees, referred to in the previous section.

VII. SIGNIFICANCE OF RESERVES AND TRANSLOCATION TO NUTRIENT MANAGEMENT AND DIAGNOSIS

Management of nutrient reserves within the tree may be desirable to reduce external nutrient demand, to control stress or disease, or perhaps to promote

a particular phase of growth, for example, reproductive rather than vegetative growth. Fertilization provides an opportunity for managing reserves within the tree. At least in the case of N, the time and method of application and the form of N, as well as quantity, affect the form and distribution of reserves. It is possible to increase nutrient reserves of planting stock, which shows pronounced winter dormancy, by applying fertilizer after shoot dormancy has developed in autumn (Anderson and Gessel, 1966; Benzian *et al.*, 1974). Accumulated nutrient reserves may improve the ability of such stock to become established and make rapid early growth after planting.

Other opportunities for management of nutrient reserves depend, at present, on choice of species, since differences in nutrient distribution and internal recycling exist between different species. There may also be differences in these characters between genotypes; for example, it has been suggested that different N and P concentrations in progeny groups of *Pinus elliottii* seedlings, receiving two levels of nutrient supply, reflected differences in ability to absorb and utilize nutrients (Walker and Hatcher, 1965). No measurements of genotypic differences in nutrient retranslocation seem to have been made although differences between needle retention of *Pinus radiata* clones have been observed (Burdon, 1976), and may be related to nutrient retranslocation. Thus more work is required to decide whether important differences in storage and retranslocation are related to genotype, and whether their usefulness can be enhanced through selection and breeding.

Definition of the times and extent of translocation into and out of different tree tissues should provide a sounder basis for interpreting tissue chemical analysis to diagnose nutrient status. Traditionally foliage of trees has been sampled during late summer (deciduous species) or late autumn (evergreens). This is perhaps based on the idea that internal nutrient status reflects the available soil nutrients more closely after the main period of seasonal growth. Certainly, changes in nutrient concentrations with time are less evident in current foliage of evergreen conifers during autumn and winter. As mentioned previously, however, in deciduous trees rapid reduction in the content of mobile nutrients occurs shortly before abscission; thus sampling takes place before retranslocation commences, but after leaf growth ceases in deciduous trees. However there is an argument for sampling foliage during the period of extension growth when expanding tissue is thought to be under maximum nutrient stress. As rapid shoot extension growth occurs in spring, foliar nutrient concentrations decline because translocation into new tissue is outstripped by growth or because retranslocation occurs (Fife and Nambiar, 1982). Nutrient analysis at this time may reveal nutrient deficiencies which are subsequently masked by continued retranslocation or uptake by the tree (van den Driessche, 1974).

Recognition that nutrients are retranslocated has also prompted the idea

that comparison of nutrient concentrations in needles and twigs of different age classes could provide more information about tree nutrient status than analysis of current tissue alone (van den Driessche, 1974). Trees under nutrient stress may show lower nutrient concentrations in older foliage because of greater retranslocation (Florence and Chuong, 1974). Such differences between young and old tissue may require further study since, for example, in K-deficient *Pinus resinosa*, K-concentration differences between current and three-year old foliage varied five-fold according to vertical position in the crown (Comerford, 1981).

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